THE ROLE OF BACTERIVOROUS AND FUNGIVOROUS NEMATODES IN CELLULOSE AND CHITIN DECOMPOSITION IN THE CONTEXT OF A ROOT/RHIZOSPHERE/SOIL CONCEPTUAL MODEL

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INTRODUCTION

Previous papers in this symposium have noted that nematodes are ubiquitous, existing in an array of terrestrial and aquatic habitats. Yeates and Coleman (this volume) reviewed the diversity of reproductive and feeding strategies that allow nematodes to utilize virtually every sort of substrate available to metazoa.

To better understand specific aspects of the role of nematodes in decomposition, workers have conducted a series of experiments in laboratories around the world of grassland (Colorado, Coleman et al. 1977, 1978), pine forest (Sweden, Bååth et al. 1978, in press), and sewage sludge-amended soils (Syracuse, New York, Abrams and Mitchell 1980). We will concentrate our report on a conceptual model of nematodes in a root/rhizosphere/soil system and on recent results from model soil microcosm systems.

Carbon Inputs and Decomposition in Grassland Soils

The soil environment can be viewed as an interconnected network of pores, varying in size and water content, through which nutrients and organisms can migrate. Maximum microfloral activity occurs at sites of monomeric and oligomeric forms of reduced carbon (especially plant material). These sites may be close to the plant, as in the rhizosphere, where root exudate or sloughed root material is present, or in senescent and dead roots (a more resistant carbon source). Other sites of reduced carbon are at heterogeneously distributed clumps of

organic matter entering the soil as litter. In the shortgrass prairie about 23% of the organic carbon enters the soil as aboveground litter, 54% as detrital roots and 23% as root exfoliates and exudates (Coleman 1976).

Coleman et al. (in press) postulate the existence of pathways of catabolism, involving labile and nonlabile substrates, rather than organism-oriented pathways. In a series of experiments Woods et al. (in press), Anderson et al. (1978), Coleman et al. (1978a,b), Cole et al. (1978), and Herzberg et al. (1978) found that combining simulated root exudate and bacteria, amoebae, and nematode grazers resulted in the marked remineralization of P and, in some instances, N, over periods of several weeks.

We extended those studies to model nonlabile substrates (chitin and cellulose), the chitinoclastic and cellulolytic microflora (bacteria and fungi), and the bacterivorous and fungivorous nematode grazers that feed upon them.

We postulated that decomposition would increase during grazing and that a significant synergism (i.e., enhanced total decomposition in the presence of two substrates or two or more species of primary decomposers) would occur, as was noted by Dommergues and Mangenot (1970).

During the experiments, we looked for the aspects of functional group dynamics that one might expect because of the diverse nature of feeding. Thus, our bacteria feeders are holophagic, digesting only about 50-80% of the food ingested (Smerda et al. 1971); whereas hyphal-feeders, have a piercing stylet, suck cell sap (cytoplasm) out of the hyphae, as do plant root feeders. The feeding mode may have a profound effect on overall metabolic activity and nutrient remineralization.

A REPRESENTATION OF A ROOT/RHIZOSPHERE/SOIL SYSTEM

Fig. 1 [representing roots in a shortgrass prairie in northeastern Colorado dominated by Bouteloua gracilis [H.B.K. (Griffiths)] (blue grama)] is a conceptual diagram of the important interactions occurring in a root/rhizosphere/soil system. The following description in conjunction with the center section of Figure 1 provides a simple illustration of the importance of different root regions.

Root/Rhizosphere

Major phenological changes occur during the growth and extension of a root. Mucigel, the zone of elongation, and root exudation are associated with the growing root tip, an area of rapid growth, sloughing of cells, and exudation of low molecular weight carbon compounds (Rovira et al. 1979). Mucigel produced at the root tip may function in several ways: as a lubricant enhancing root penetration through the soil; as a medium through which extracellular enzymes of root or microbial origin diffuse to come in contact with clay-fixed or particulate sources of substrate; and as a source of substrates for growing microflora, which may protect the root by screening it from plant pathogens (Atkinson et al. 1972).

A root hair zone develops behind the root tip and could enhance nutrient uptake either due to the increased surface area of the root hairs (Brady 1974) and/or by anchoring the root to maintain close contact with the soil (Newman 1974).

Within the root hair zone and as the root ages, mycorrhiza (endomycorrhizae in the diagram) are formed with particular species of symbiotic fungi, well known to enhance P (Rhodes and Gerdemann 1980) and perhaps N uptake (Pang and Paul 1980) for the plant in exchange for reduced carbon from the plant.

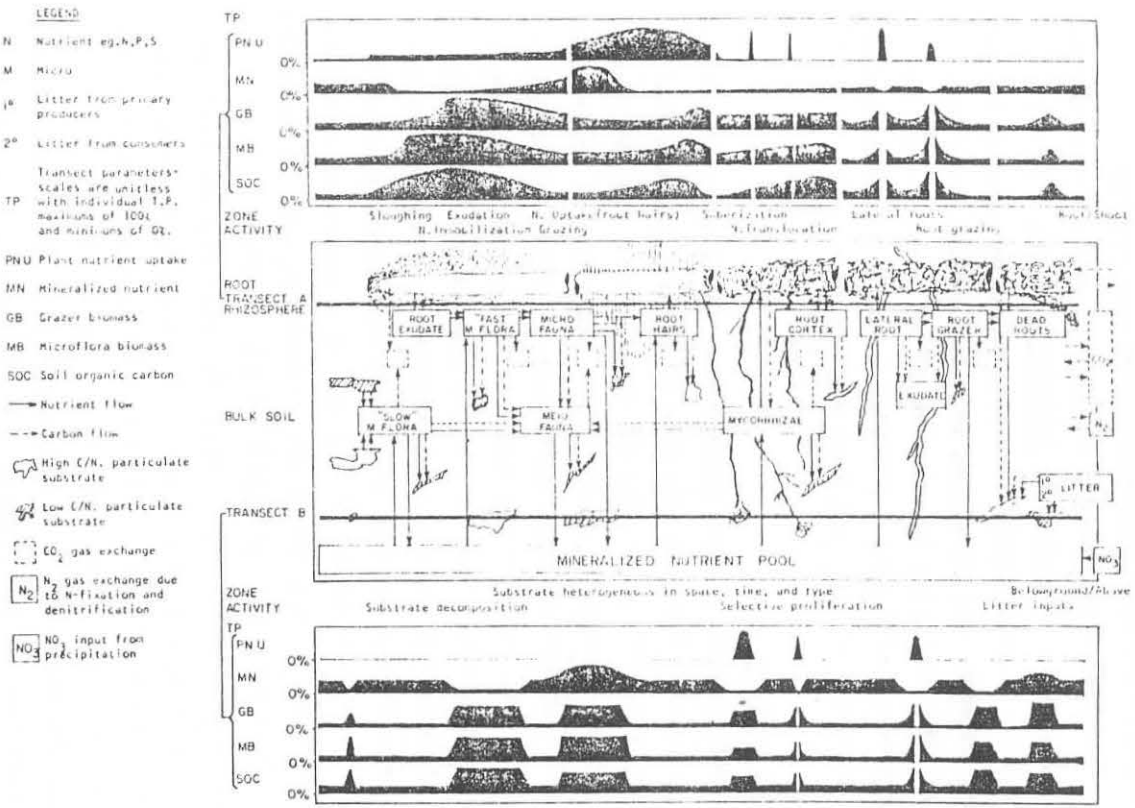

Fig. 1. Conceptual diagram of a root/rhizosphere/soil system. Refer to text for explanation.

As the root becomes suberized, lignin and cellulose content increases (Coleman 1976), mineral nutrient uptake ability decreases, and cortical cells are sloughed, releasing nonlabile forms of carbon. Development of new lateral roots renews the nutrient uptake capabilities of the root and increases the level of labile carbon in the soil (Coleman 1976). Death of roots provides an input of resistant, high C to N ratio (C:N) substrate.

The following is a brief description of how root exudate might enhance nutrient availability to the plant. Reference should be made to the transect through the rhizosphere (Transect A, Fig. 1) parallel to a growing root and to the idealized relative levels of soil organic carbon (SOC), microfloral biomass (MB), grazer biomass (GB), mineralized nutrient (MN), and rate of plant nutrient uptake (PNU) in the expanded transect (upper graphs, Fig. 1). High C:N primarily monomeric material produced at the root tip (Fig. 1, SOC) is readily metabolized by microbes. The populations rapidly increase, immobilizing any (Fig. 1, MN) nutrient in or diffusing to the root region and any available organic form of the nutrient. The increase in microfloral biomass (Fig. 1, MB) stimulates the microfauna (Fig. 1, GB) populations which begin to mineralize nutrients (Coleman et al. 1978a). As long as sufficient carbon is available, nutrients will remain immobilized, primarily in microfloral biomass. However, the root extends and matures, the zone of peak exudation moves away with the extending root, and the microhabitat becomes drier as water is taken up by the plant. The microfauna, mineralizing nutrients, continue to graze on the declining populations of microflora then either encyst or migrate. Nutrients are mineralized (Fig. 1, MN, beginning of root hair zone) when the root hairs begin to develop, thereby increasing the pool of nutrients available for plant uptake.

Death of the root hairs (Fig. 1; end of root hair zone) provides a pulse of easily assimilated carbon, briefly increasing microflora and -fauna populations. Because they are less labile, cortical cells (Fig. 1, root cortex) sloughed during suberization will support a lower, slower-growing microbe population. Organisms capable of decomposing such materials as lignin and cellulose will predominate where those substrates are the major components of the organic matter (Alexander 1977). Young lateral roots would have similar effects to those described for young primary roots.

Root grazers (e.g., ectoparasitic nematodes), occurring primarily with young unsuberized roots, add to the pool of plant-derived soil carbon (Fig. 1, root grazer). Excretory products, "leaks" from the root caused by injury to the root, and dead roots all add to the available pool of organic soil carbon.

Bulk Soil

A major portion of the soil organic carbon occurs away from the root in the bulk soil and is in a more resistant particulate form. An idealized transect through this area (Fig. 1, Transect B and its expansion) would show microflora associated primarily with the "islands" of organic matter. Depending on the origin, C:N, and history of the organic matter, nutrients at these sites would be either immobilized or mineralized. Sites of particulate organic matter supporting large microfloral populations could attract and support micro- and meiofaunal populations.

Mycorrhizal fungi may selectively proliferate (Fig. 1) where a nutrient is being mineralized, and bacterial activity may increase next to hyphae because of hyphal exfoliates or other material from hyphal walls.

The box and arrow diagram in Fig. 1 summarizes some of the major flows of carbon and nutrients between the biotic and mineral components of a root/rhizosphere/soil system. The meiofauna and the mycorrhizal fungi can be viewed as "shunts" between the labile and nonlabile pathways of catabolism. Meiofauna disperse primary decomposers (Powell 1971) and translocate nutrients and carbon as biomass. The mycorrhizal fungi translocate nutrients from the bulk soil to the root; and, when the hyphae die, their biomass (of plant-derived carbon) becomes part of the bulk soil.

DECOMPOSITION EXPERIMENTS

A review of a few of our nonlabile substrate decomposition experiments at Colorado State University follows:

Substrates

Because a large part of the vegetation added to soil is cellulosic, the decomposition of this carbohydrate has special significance in carbon cycling. Cellulose consists of long, linear chains of glucose units bound together in β-linkages at carbon atoms 1 and 4. Typically, 2,000 to 10,000 glucoside residues are linked in one chain (Sihtola and Neimo 1975). Elementary chains do not typically exist in native cellulose but tend to form fibrils, in which polymer chains are oriented in parallel and are firmly bound together by a large number of strong hydrogen bonds. The fibrils are arranged in higher-order bundles, which may be structurally interlinked with lignin in plant cell walls.

The cellulose used in these experiments was a purified microcrystalline cellulose with particle sizes of 5-20 μm (Whatman #CC41 Cellulose Powder).

Chitin is a structural compound in the cell walls of filamentous fungi, egg shells of nematodes, and the exoskeleton of arthropods (Muzzarrelli 1977). Because chitin is high in nitrogen (C:N≅6·6) and much of it is formed by microbial biosynthesis, it is undoubtedly an important substance in the carbon cycle in the soil. Chitin is a long, linear chain of N-acetylglucosamine units, a polymer similar to cellulose, except that one of the hydroxyl groups of each glucoside residue is replaced by an acetyl amino group. Individual chains can be bound, in parallel or antiparallel, into microfibrils of varying crystalline states and hence decomposability. Arthropod cuticle is a composite material with microfibrils of α-chitin (mostly crystalline) randomly embedded in a protein matrix.

The chitin used in these experiments was from a crustacean cuticle that was washed in an acid-alkaline solution and ball-milled (described in Gould et al., in press).

Organism Isolations

Chitin- and cellulose-decomposing bacteria, fungi, and actinomycetes were isolated from soils of the Pawnee National Grasslands, a shortgrass prairie in northeastern Colorado dominated by Bouteloua gracilis. The decomposers were isolated by enriching the soil with cellulose or chitin or by a buried slide technique (Parkinson et al. 1971), then tested for their relative abilities to decompose chitin (NACG production, Reissing et al. 1955) and cellulose (Agar-diffusion assay, Tansey 1971).

Palatibility studies were conducted using the bacterial isolates and a Pelodera sp. isolated from the chitin enrichment. Nematodes were sterilized by passing an adult female through alternate series of wells containing dilute (1/2 strength) nutrient broth with or without an antibiotic mixture of streptomycin sulfate, penicillin, and fungizone. Aphelenchus avenae

cultures on Rhizoctonia solani, obtained from D. Freckman, University of California at Riverside, were cleaned and transferred to a Fusarium oxysporum isolated from a soil enrichment. A. avenae occurs abundantly in the native soil (Smolik, unpublished data).

Microcosm Design and Sampling

The organisms were inoculated into 50-ml Erlenmeyer flasks containing 20 g of soil from the Renohill-Shingle complex, a sandy loam from the Pawnee Grasslands. The soil was moistened and autoclaved twice at 24-h intervals, amended with cellulose or chitin, or both, autoclaved a third time, and dried. One ml of a washed liquid culture of bacteria (Flavobacterium sp.) or fungi (F. oxysporum) was inoculated into the microcosms. The soil was brought to 15% moisture w/v (field capacity) with a mineral salts solution (RSS, Herzberg et al. 1978) with or without an ammonium sulfate nitrogen amendment. The microcosms were sealed in 500-ml Mason jars containing 1.8 ml of 1 N NaOH to absorb CO_2. The frequency of the titrations of the NaOH was initially every 24 h but was decreased as the level of respiration decreased. Nematode grazers were inoculated into the systems 2-4 d after the microflora were inoculated.

Three replicate microcosms were destructively sampled at the completion of each experiment. In some experiments, additional microcosms were prepared to allow sampling during the experiment. Analyses were made of NH_4^+-N (modified Conway, Stanford et al. 1973), inorganic P (bicarbonate extractable, Olsen et al. 1954), bacteria populations (soil dilutions plated on nutrient agar), gravimetric soil moisture, nematode numbers (modified Baerman, Anderson and Coleman 1977) and, in some cases, chitin remaining in the soil (alkaline distillation, Bremner and Shaw 1954).

Chitin Decomposition

Chitin was added to the microcosms at a level of 3000 μg chitin-C·g^{-1} dry soil. Microcosms were destructively sampled on days 24, 37, 80. By day 80 significantly more chitin was decomposed and more NH_4^+-N mineralized in the Fusarium treatment than in either the grazed or ungrazed bacteria treatments (Fig. 2). Nematode-grazed bacteria (Flavobacterium sp.) mineralized a significant amount of N from native organic-N sources (Fig. 2). Bacterial populations were initially higher in the grazed treatments but decreased as the nematode population increased (Fig. 3). Bacterial biomass may have increased in the presence of nematodes because of the bacteria's utilization of nematode excretory and fecal products, particularly amino acids (Anderson et al., submitted). In addition, the nematodes could disperse bacteria (Anderson et al., in press) adsorbed on the nematode's cuticle (Powell 1971). Increased metabolic activity in the presence of a grazer has been observed several times (Coleman et al. 1977, Anderson et al. 1978, Coleman et al. 1978a, Elliott et al. 1980) and is attributed to the grazer's keeping the bacteria population in more active growth phases.

Cellulose Decomposition

Cellulose additions of 800 μg cellulose-C·g^{-1} dry soil were made to all microcosms, half of which received additions of 115 μg $(NH_4)_2SO_4$-N·g^{-1} dry soil. Addition of NH_4^+ increased the level of C mineralization by the bacteria (Fig. 4) to the level in microcosms with nematode-grazed bacteria. By the end of the experiment the unamended nematode-grazed bacterial treatment had mineralized significantly more of the native organic-N (Table 1) and had higher numbers of bacteria than the bacteria-alone treatments. Carbon mineralization in the N-amended

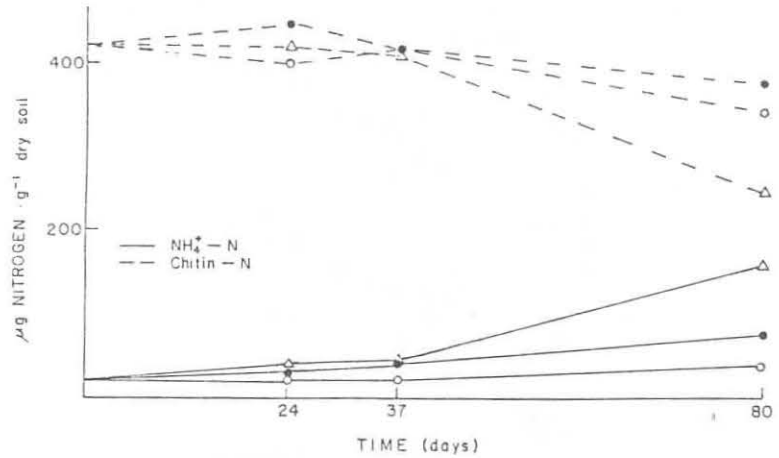

Fig. 2. Mean levels of chitin (---) and (——) NH_4^+-N in the chitin decomposition experiment. Δ = Fungus, O = Ungrazed bacteria, ● = Nematode grazed bacteria treatment.

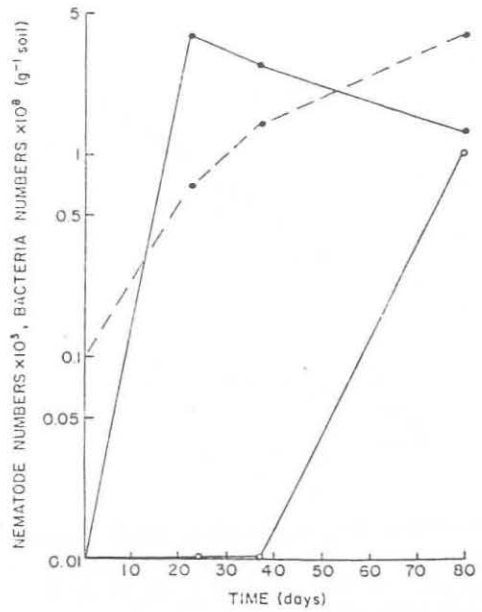

Fig. 3. Mean bacteria (——) and nematode (---) numbers in the chitin decomposition experiment. O = Ungrazed bacteria, ● = Nematode grazed bacteria.

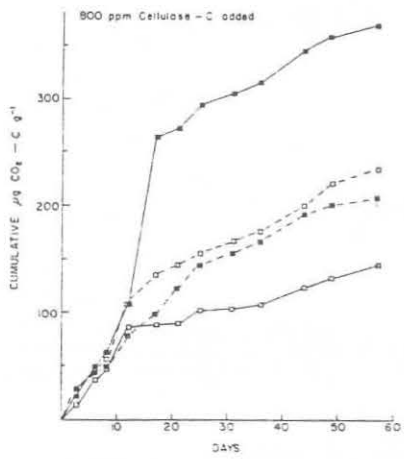

Fig. 4. Mean cumulative CO_2 evolution from bacterial treatments in the cellulose decomposition experiment with (---) and without (——) the addition of 115 µg $(NH_4)_2SO_4$-N·g^{-1}. □ = Ungrazed bacteria, ■ = Nematode grazed bacteria.

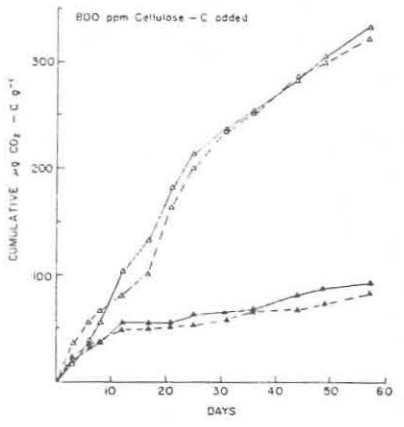

Fig. 5. Mean cumulative CO_2 evolution from fungal treatments in the cellulose decomposition experiment with (---) and without (——) the addition of 115 µg $(NH_4)_2SO_4$-N·g^{-1}. △= Ungrazed fungus, ▲= Nematode grazed fungus.

TABLE 1. Decomposition of Cellulose in Microcosms With and Without Nitrogen Amendments. Treatments Include Microflora Alone and in Combination With Adult or Juvenile Microbivorous Nematodes. Values are Means of Three Replicates.

Treatment	Counts of Organisms	NH_4^+-N ($\mu g/g$)	Pi ($\mu g/g$)
No nitrogen added			
Bacteria (*Flavobacterium* sp.)	$76 \cdot 10^5 \cdot g^{-1}$	22	19
Bacteria *Pelodera* sp.	$838 \cdot 10^5 \cdot g^{-1}$		
" "	108 Adults$\cdot g^{-1}$	34	19
" "	370 J_2-$J_4 \cdot g^{-1}$		
Fungus (*Fusarium oxysporum*)	--	32	18
Fungus with *A. avenae*	--		
" "	$9 \cdot g^{-1}$	24	18
Uninoculated control	--	24	18
115 ppm ammonium sulfate-N			
Bacteria	$306 \cdot 10^5 \cdot g^{-1}$	133	17
Bacteria with *Pelodera* sp.	$434 \cdot 10^5 \cdot g^{-1}$		
" "	36 Adults$\cdot g^{-1}$	140	17
" "	189 J_2-$J_4 \cdot g^{-1}$		
Fungus	--	159	19
Fungus with *A. avenae*	--		
" "	$4 \cdot g^{-1}$	136	19
Uninoculated control	--	139	17

grazed system was not significantly different from that in the ungrazed systems perhaps because of the toxic effects of ammonia on the nematodes, reflected, perhaps, in lowered nematode numbers. The amount of C mineralized by the fungi was unaffected by the N amendment (Fig. 5). In contrast to the bacteria-grazed and -ungrazed systems, significantly less C was mineralized by the nematode-grazed hyphae than by the fungi alone. Large nematode inoculations (25 individuals$\cdot g^{-1}$), combined with a short initial incubation period for fungi (48 h), may have resulted in the fungi's being overgrazed. The fungi mineralized a significant amount of native organic-N (Table 1).

Decomposition of Cellulose and Chitin

Cellulose (314 μg C-g^{-1} dry soil) was added to all microcosms; some microcosms received an additional amendment of 686 μg chitin-C·g^{-1} dry soil (total C = 1000 μg; C:N = 10:1). Throughout the experiment significantly more N was mineralized in the nematode-grazed bacteria treatment than in the ungrazed treatment (Fig. 6). As was seen in the previous experiments, nematode grazed bacterial populations (Fig. 7) were initially higher than ungrazed. A bacterial contaminant unable to decompose cellulose or chitin was introduced with the fungus grazer A. avenae. Presumably, the bacteria could compete with the fungi for limiting nutrients or for breakdown products produced by fungal chitinase. Even with substantial bacteria populations (Fig. 7) the grazed-fungus treatment mineralized more N than the ungrazed treatment (Fig. 8). The nematode-grazed bacteria mineralized more N than either of the fungus treatments.

In the cellulose alone-amended microcosms about 300 μg of CO_2-C·g^{-1} dry soil was respired in all biological treatments except the bacteria-alone treatment (Fig. 9). Microcosms containing the most complex biota had higher initial rates of CO_2 evolution but the rate decreased earlier than in microcosms containing the fungal and grazed bacteria treatments. Microcosms with a cellulose and chitin amendment evolved more CO_2 (Fig. 10) than the same biological treatment with cellulose alone (Fig. 9), except for the ungrazed bacteria treatment, where no significant difference in CO_2 evolution occurred. The treatment with the most complex biotic treatment mineralized significantly more C than any of the other treatments. In both C amendments the nematode-grazed bacteria respired more than the ungrazed bacteria.

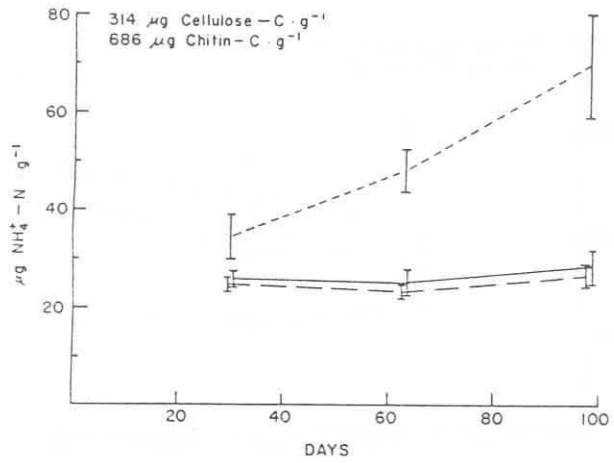

Fig. 6. Mean soil NH_4-N levels with 95% confidence intervals in bacterial treatments of the cellulose and chitin decomposition experiment. ——— = Ungrazed bacteria, --- = Nematode grazed bacteria, — — — = Uninoculated control.

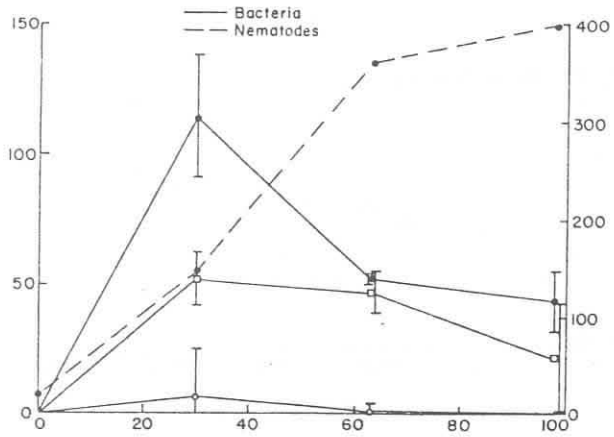

Fig. 7. Mean bacteria (———) and nematode (---) numbers with 95% confidence intervals for treatments in the cellulose and chitin decomposition experiment. ○ = Ungrazed bacteria, ● = Nematode grazed bacteria, □ = Contaminating bacteria in the nematode grazed fungus treatment.

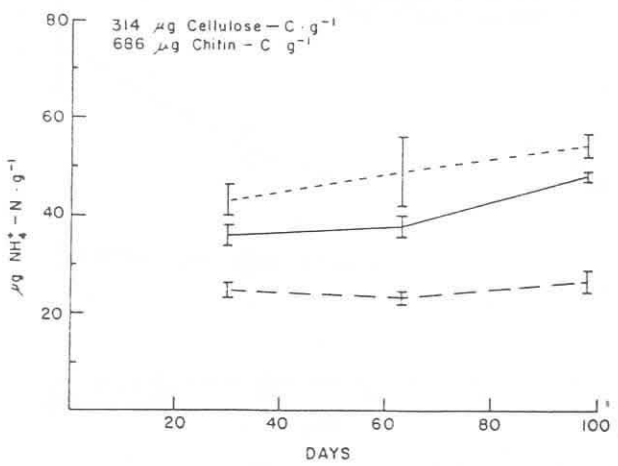

Fig. 8. Mean soil NH_4^+-N levels with 95% confidence intervals in fungal treatments of the cellulose and chitin decomposition experiment. —— = Ungrazed fungus, --- = Nematode grazed fungus, — — — = Uninoculated control.

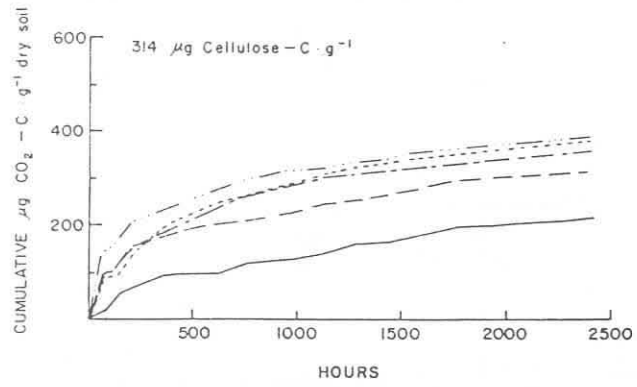

Fig. 9. Mean cumulative CO_2 evolution from microcosms containing 314 µg cellulose-C·g^{-1} amendment in the cellulose and chitin decomposition experiment. —— = Ungrazed bacteria, --- = Nematode grazed bacteria, — — = Ungrazed fungus, — - — = Nematode grazed fungus, —··· — = Nematode grazed bacteria with nematode grazed fungus.

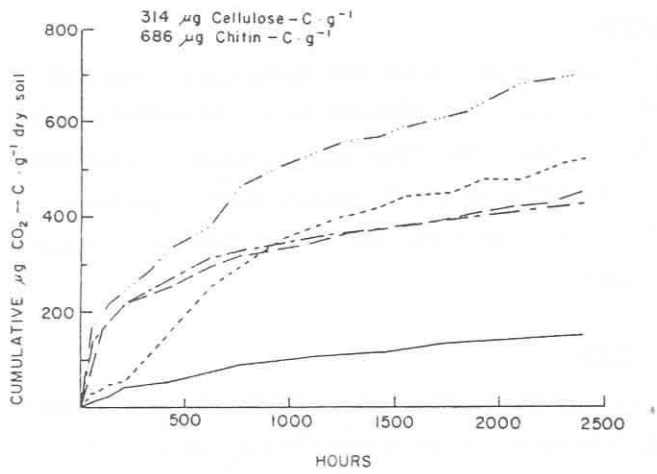

Fig. 10. Mean cumulative CO_2 evolution from microcosms containing 314 μg cellulose-C·g^{-1} and 686 μg chitin-C·g^{-1} amendment in the cellulose and chitin decomposition experiment.
——— = Ungrazed bacteria, --- = Nematode grazed bacteria,
— — = Ungrazed fungus, — - — = Nematode grazed fungus,
—••— = Nematode grazed bacteria with nematode grazed fungus.

In summary, in some cases nematode grazers can increase the rate of organic matter decomposition. This could occur by maintaining microfloral populations in a log phase growth, by mineralizing nutrients that would otherwise remain immobilized in stationary-phase microflora, or by dispersing relatively immobile microflora. In other instances, if microbial populations (particularly fungi) are very heavily grazed, system-level activity may be significantly inhibited.

ACKNOWLEDGMENTS

This research was supported by NSF Research Grants DEB 78-11201 and 80-04193. Thanks are extended to C. Cambardella, C. R. Morley, R. Hays, and J. S. Frey for technical assistance. We also thank E. T. Elliott, W. D. Gould, R. V. Anderson, C. R. Morley and T. V. St. John for their contributions towards the conceptual model.

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